A new postcranium of Saurichthys from the Early Triassic of Spitsbergen

Kogan, Ilja ; Romano, Carlo

Abstract: The Saurichthyidae (Actinoperygii, Osteichthyes) are a long-lasting family, ranging from the latest Permian to the Middle Jurassic (75 million years) and including nearly 50 species, most of which belong to the essentially Triassic genus Saurichthys. At least 14 species occur in the Early Triassic, but many of them are only scarcely known, leading to a gap of knowledge of their early evolution. Four species have been described from the Early Triassic of Spitsbergen (Svalbard archipelago, Arctic Norway): Saurichthys wimani, S. ornatus, S. elongatus and S. hamiltoni. These taxa are based predominantly on cranial material, whereas postcrania, which contain more diagnostic features in Saurichthys, are extremely rare. We present the eighth saurichthyid postcranium from Spitsbergen, which was collected during the 2008 Swiss-Norwegian expedition to Stensiöfjellet (Mount Stensiö), Sassendalen. The new specimen is the most complete saurichthyid postcranial segment known from Spitsbergen, preserving the portion between the pelvic girdle and the caudal fin, and is ascribed to S. wimani based on the squamation. S. wimani can now be characterized by the following set of postcranial traits: (1) all fins with segmented and branched lepidotrichia and fringing fulcra along their leading edge, (2) rows of large, ornamented scales in mid-dorsal, mid-ventral and mid-lateral position and small, rhombic dorsolateral scales (the ventrolateral scale row being probably absent), and (3) a vertebral column consisting of (dorsal) neural arches with small praeand postzygapophyses and distinct neural spines, relating as 2:1 to the mid-lateral scales, and to the (ventral) haemal arches as 2:1 in the abdominal and as 2:2 in the caudal body portion. Mid-lateral scales of the caudal peduncle bear denticles on their ventrocaudal margin, previously unknown in saurichthyids. At least three species of Saurichthys are distinguishable in the Smithian aged 'fish horizon' of Spitsbergen based on postcranial characters, supporting a fast diversification of saurichthyids following the great end-Permian mass extinction event.

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by Ilja Kogan (Freiberg) & Carlo Romano (Zürich)
with 6 figures

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Contents:

Abstract

The Saurichthyidae (Actinoperygii, Osteichthyes) are a long-lasting family, ranging from the latest Permian to the Middle Jurassic (~75 million years) and including nearly 50 species, most of which belong to the essentially Triassic genus *Saurichthys*. At least 14 species occur in the Early Triassic, but many of them are only scarcely known, leading to a gap of knowledge of their early evolution. Four species have been described from the Early Triassic of Spitsbergen (Svalbard archipelago, Arctic Norway): *Saurichthys wimani*, *S. ornatus*, *S. elongatus* and *S. hamiltoni*. These taxa are based predominantly on cranial material, whereas postcrania, which contain more diagnostic features in *Saurichthys*, are extremely rare. We present the eighth saurichthyid postcranium from Spitsbergen, which was collected during the 2008 Swiss-Norwegian expedition to Stensiöfjellet (Mount Stensiö), Sassendalen. The new specimen is the most complete saurichthyid postcranial segment known from Spitsbergen, preserving the portion between the pelvic girdle and the caudal fin, and is ascribed to *S. wimani* based on the squamation. *S. wimani* can now be characterized by the following set of postcranial traits: (1) all fins with segmented and branched lepidotrichia and fringing fulcra along their leading edge, (2) rows of large, ornamented scales in mid-dorsal, mid-ventral and mid-lateral position and small, rhombic dorsolateral scales (the ventrolateral scale row being probably absent), and (3) a vertebral column consisting of (dorsal) neural arches with small prae- and postzygapophyses and distinct neural spines, relating as 2:1 to the mid-lateral scales, and to the (ventral) haemal arches as 2:1 in the abdominal and as 2:2 in the caudal body portion. Mid-lateral scales of the caudal peduncle bear denticles on their ventrocaudal margin, previously unknown in saurichthyids. At least three species of *Saurichthys* are distinguishable in the Smithian aged 'fish horizon' of Spitsbergen based on postcranial characters, supporting a fast diversification of saurichthyids following the great end-Permian mass extinction event.

Zusammenfassung

Die Saurichthyidae (Actinoperygii, Osteichthyes) waren eine langlebige, vom spätesten Perm bis in den Mittleren Jura (~75 Millionen Jahre) reichende Familie, die fast 50 Arten umfasst, von welchen die meisten zu der im Wesentlichen triassischen Gattung *Saurichthys* gehören. Mindestens 14 Arten kommen bereits in der frühen Trias vor, sind aber größtenteils unzureichend bekannt, so dass eine Wissenslücke hinsichtlich der frühen Evolution der Saurichthyiden besteht. Aus der frühen Trias Spitzbergens (Norwegische Arktis) sind vier Arten beschrieben worden: *Saurichthys wimani*, *S. ornatus*, *S. elongatus* und *S. hamiltoni*. Diese Taxa sind mehrheitlich auf Schädelresten begründet, wohingegen Postkrania, die bei *Saurichthys* mehr diagnostische Merkmale aufweisen als Schädel, extrem selten sind. Wir beschreiben das achte Postkranium eines Saurichthyiden von Spitzbergen, das 2008 während der Schweizerisch-Norwegischen Expedition zur Lokalität Stensiöfjellet (Stensiö-Berg), Sassendalen, geborgen wurde. Das neue Exemplar ist das bisher vollständigste Saurichthyiden-Postkranium von Spitzbergen – es reicht von kurz vor dem Beckengürtel bis zur Schwanzflosse – und kann anhand der Beschuppung *S. wimani* zugeschrieben werden. *S. wimani* kann somit anhand folgender postkranialer Merkmale charakterisiert werden: (1) alle Flossen mit segmentierten und verzweigten Flossenstrahlen und mit säumenden Fulkren entlang des Flossenvorderrandes, (2) große, ornamentierte Schuppen, angeordnet in Längsreihen in mittdorsaler, mittventraler und mittlateraler Lage, sowie kleine, rhomboide Schuppen in dorsolateraler Position (eine ventrolaterale Schuppenreihe ist wahrscheinlich nicht ausgebildet), und (3) ein Axialskelett bestehend aus (dorsalen) Neuralbögen mit kurzen Prä- und Postzygapophysen und deutlich ausgeprägten Neuralfortsätzen, die sich wie 2:1 zu den Mittlateral-Schuppen verhalten und zu den (ventralen) Hämalbögen im Abdominalabschnitt in einem 2:1-Verhältnis und im Kaudalabschnitt in einem 2:2-Verhältnis stehen. Der ventrokaudale Rand der Mittlateral-Schuppen im Schwanzstiel trägt Dentikel, wie sie bei Saurichthyiden bisher nicht bekannt waren. Zumindest drei *Saurichthys*-Arten können innerhalb des 'Fischniveaus' (Smithium) Spitzbergens anhand postkranialer Merkmale unterschieden werden – ein Befund, der eine rasche Diversifikation der Saurichthyidae nach dem größten Massenaussterbeereignis am Ende des Perms unterstützt.

1 Introduction

With almost 50 species, known from latest Permian to early Middle Jurassic strata worldwide, the Saurichthyidae represent one of the most-speciose and most-widespread 'palaeopterygian' (non-neopterygian actinopterygian) families of the early Mesozoic (e.g. ROMANO et al., 2012; KOGAN & ROMANO, 2016; MAXWELL, 2016). The distinctive morphology and often large body size (up to more than 1.5 m; e.g. STENSIÖ, 1925; MUTTER et al., 2008; TINTORI, 2013) qualify saurichthyids as high-level predators in both marine and freshwater environments and, thus, ideal study animals in the context of aquatic faunal transformations during the latest Permian and Triassic upheavals. However, many species have been described decades ago and need restudy in light of newly obtained comparative data. This is especially true for saurichthyids from the Early Triassic, which are crucial for the understanding of the early evolution of the group, yet still insufficiently known (KOGAN & ROMANO, 2016).

The Arctic Island of Spitsbergen (Svalbard archipelago, Norway; Fig. 1) is one of the classic marine localities for Early Triassic vertebrates (BRINKMANN et al., 2010; KEAR, et al., 2016), yielding various fishes and tetrapods (e.g. WIMAN, 1910, 1933; WOODWARD, 1912; STENSIÖ, 1918, 1921, 1925, 1932; COX & SMITH, 1973; BIRKENMAJER & JERZMAŃSKA, 1979; VÉRAN, 1988, 1995, 1996; BŁAŻEJOWSKI, 2004; ROMANO & BRINKMANN, 2010; MAXWELL & KEAR, 2013; SCHEYER et al., 2014a). The fish assemblages of Early Triassic (Dienerian, Smithian, Spathian) age contain chondrichthyans (hybodontiforms, neoselachians, eugeneodontids), dipnoans, actinistians, but above all actinopterygians (Table 1). Articulated fish material is derived predominantly from the so-called 'fish horizon' (STENSIÖ, 1921) and comprises, among others, the genera *Birgeria*, *Bobasatrania*, *Boreosomus* and *Saurichthys* – typical representatives of the 'Triassic Early Fish Fauna' of TINTORI et al. (2014a), which became prevalent worldwide in the aftermath of the end-Permian mass extinction event (ROMANO et al., 2016).

No less than four species of *Saurichthys* have been described from the Early Triassic of Spitsbergen (WOODWARD, 1912; STENSIÖ, 1925). Although these descriptions are still largely accurate from today's perspective, they are limited by the scarce comparative material available at the time of publication and the mode of preservation in concretions, which is typical for Early Triassic fish localities (TINTORI et al., 2014a). The fossilisation in mostly small to medium-sized concretions reduces the likelihood to find whole-body fossils of elongate animals like *Saurichthys*. Indeed, the Spitsbergen saurichthyids are represented by dozens of isolated, published and unpublished skulls stored in several collections, as opposed to merely seven postcranial fragments hitherto mentioned by WOODWARD (1912) and STENSIÖ (1925).

Here we describe a new postcranium of a saurichthyid from the Early Triassic of Spitsbergen, which represents the most complete postcranial remain known so far and is the first specimen to show the caudal peduncle and fin. The fossil is compared with previously documented postcranial fragments from Spitsbergen and postcrania of selected Early and Middle Triassic saurichthyids. Postcrania contain more diagnostic characters than skulls in *Saurichthys* and are also more informative with regard to evolution and functional morphology (e.g. TINTORI et

al., 2014b; KOGAN & ROMANO, 2016). Hence, the new specimen contributes significantly to our knowledge of *Saurichthys* from Spitsbergen and early saurichthyids in general.

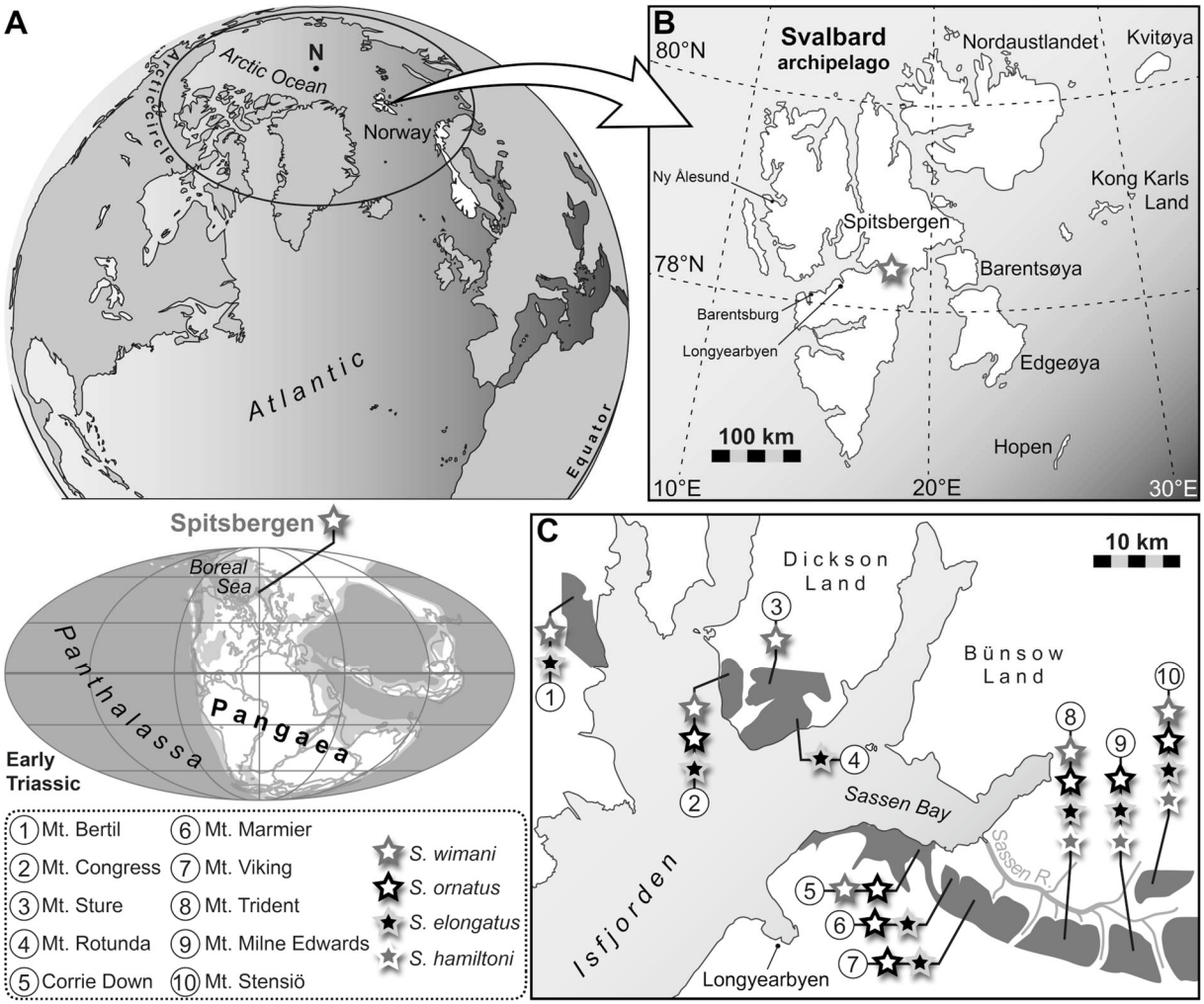


Fig. 1: A – location of Spitsbergen (Svalbard archipelago, Norway), today (above) and during the Early Triassic (below, modified from PALEOMAP project, www.scotese.com); B – map of Svalbard, with the position of the study site Stensiöfjellet (Mount Stensiö) in east-central Spitsbergen indicated by the star; C – enlarged map of Isfjorden and Sassendalen (Sassen Valley) in central and east-central Spitsbergen, with Triassic outcrops roughly indicated in dark grey (modified from STENSIÖ, 1921). The occurrences of the four species of *Saurichthys* are mapped in (C) after WOODWARD (1912), STENSIÖ (1925), and this study (occurrences of *Saurichthys* sp. after STENSIÖ, 1925 omitted).

2 Material and Methods

The fossil described below is stored at the Palaeontological Institute and Museum, University of Zurich (PIMUZ), Switzerland, and has the collection number PIMUZ A/I 4363. The specimen was found in August 2008 during the Swiss-Norwegian expedition to the island of Spitsbergen (Fig. 1), east-northeast of the field camp site (see ROMANO & BRINKMANN, 2010) on the western slope of Stensiöfjellet (Mount Stensiö, or Mount Andersson in older literature, WIMAN, 1910; STENSIÖ, 1921; BUCHAN et al., 1965). Apart from new trematosaurid 'amphibian' remains (stored at the Natural History Museum, University of Oslo, Norway), this expedition yielded primarily invertebrate and fish material (curated in the PIMUZ), among others a new partial skeleton of the hybodont chondrichthyan *Palaeobates polaris* STENSIÖ, 1921 (ROMANO & BRINKMANN, 2010), and one of the largest known skulls of the predatory actinopterygian *Birgeria* STENSIÖ, 1919 (PIMUZ A/I 4301; partly illustrated by SCHEYER et al., 2014a).

Tab. 1: Occurrences of osteichthyan taxa in different Triassic levels of Svalbard, compiled after WOODWARD (1912), STENSIÖ (1918, 1921, 1925, 1932), FREBOLD (1935), SCHWARZ (1970), COX & SMITH (1973), BIRKENMAJER & JERZMAŃSKA (1979), BŁAŻEJOWSKI et al. (2013), SCHEYER et al. (2014a) and references therein. Stratigraphy after WIMAN (1933), FREBOLD (1935), WEITSCHAT & DAGYS (1989), MØRK et al. (1999), MØRK & WORSLEY (2006) and references therein. For a list of occurrences of Chondrichthyes in the Early Triassic of Spitsbergen see ROMANO & BRINKMANN (2010). A = Actinopterygii, S = Sarcopterygii, * = isolated teeth/scales only; ** = quality of material unspecified.

Stage	Formation (Member)	Horizon	Osteichthyan taxa
?	?	'Upper bone bed in the Upper Triassic	A *Birgeria* sp.*
Ladinian–Carnian	De Geerdalen Fm	'Upper saurian horizon'	A *Boreosomus* sp. A *Birgeria* sp.* S Actinistia indet.**
Spathian	Vikinghøgda Fm (Vendomdalen Mb)	'Below the lower saurian horizon'	S *Ceratodus* sp.* S Actinistia indet.** A *Boreosomus* ? sp. (*B.* ? *scaber*)*
			A *Saurichthys* sp.**
		?	A *Birgeria* ? sp.**
		?	A *Birgeria* sp.
		'Bone bed 50 m above the fish horizon'	A *Pteronisculus* sp. (*P. gyrolepidoides*)*
		'Bone bed 33 m above the fish horizon'/'*Grippia* horizon'	A *Birgeria* sp. (*B. mougeoti*)*
			A *Pteronisculus* sp. (*P. gyrolepidoides*)*
		?	A *Boreosomus* ? sp. (*B.* ? *scaber*)*
?	Vikinghøgda Fm	'Somewhat above the fish horizon'	A *Saurichthys elongatus* ? S Actinistia indet.**
Smithian	Vikinghøgda Fm (Lusitaniadalen Mb)	'Fish horizon' (~'*Posidonomya* beds')	S *Wimania sinuosa* S *Wimania* ? sp. S *Wimania* ? *multistriata* S *Sassenia tuberculata* S *Sassenia* ? *guttata* S *Sassenia* sp. S *Axelia robusta* S *Axelia elegans* S *Mylacanthus lobatus* S *Mylacanthus spinosus* S *Scleracanthus asper* S *Mylacanthus* ?/*Scleracanthus* ? sp. A *Birgeria aldingeri* (*B. mougeoti*) A *Birgeria* sp. A *Pteronisculus gyrolepidoides* A *Pygopterus degeeri* A *Boreosomus arcticus* A *Boreosomus reuterskioldi* A *Boreosomus* ? *scaber* A *Acrorhabdus bertili* A *Acrorhabdus asplundi* A *Acrorhabdus latistriatus* A *Bobasatrania nathorsti* A *Bobasatrania* sp. A "*Perleidus*" *woodwardi* A *Saurichthys wimani* A *Saurichthys ornatus* A *Saurichthys ornatus* ? A *Saurichthys elongatus* A *Saurichthys hamiltoni* A *Saurichthys hamiltoni* ? A *Saurichthys* sp. A "Semionotidae indet."
		'Strata immediately below the fish horizon'	A *Bobasatrania* sp.*
?	?	'Wirén's and Andersson's bone bed'	A *Saurichthys* sp.*
?	?	'Salomon's Lower Triassic bone bed'	A *Birgeria* sp. (*B. mougeoti*)* A *Pteronisculus* sp. (*P. gyrolepidoides*)* A *Boreosomus arcticus*
Dienerian	Vardebukta Fm	'Brevassfjellet *Myalina* bed(s)'	A *Saurichthys* sp.* A *Pteronisculus* sp. (*P. gyrolepidoides*)* A *Boreosomus* sp. (*B. arcticus*)*

The material of the 2008 expedition is derived from the 'fish horizon' (STENSIÖ, 1921; 'Fischniveau' of WIMAN, 1910), exposures of which extend over vast areas on Spitsbergen (FREBOLD, 1935; BUCHAN et al., 1965). The 'fish horizon' belongs to the upper part of the Smithian (early Olenekian) Lusitaniadalen Member (lower part of the Sticky Keep Member) of the marine Vikinghøgda Formation (MØRK et al., 1999; MØRK & WORSLEY, 2006).

Traditionally, two ammonoid zones have been recognized within the Lusitaniadalen Member: the early Smithian *Euflemingites romunderi* Zone and the late Smithian *Wasatchites tardus* Zone (WEITSCHAT & DAGYS, 1989; MØRK et al., 1999; BRÜHWILER et al., 2011; JATTIOT et al., 2015). Ammonoids of both zones occur on Stensiöfjellet. Vertebrate and invertebrate fossils from the 'fish horizon' are preserved in nodules and are usually found as float (e.g. STENSIÖ, 1921). Index fossils associated with the fishes are rarely mentioned in the literature; however, late Smithian ammonoids (*Wasatchites*, *Anasibirites*) are preserved with *Palaeobates polaris* (PMU P.107; ROMANO & BRINKMANN, 2010), *Saurichthys ornatus*? STENSIÖ, 1925 (PMU P.338), *Birgeria aldingeri* SCHWARZ, 1970 (PMU P.1421), *Birgeria* sp. (PIMUZ A/I 4301) and other unlabelled fish fossils collected during the 2008 expedition (R. JATTIOT, pers. comm.). The late Smithian coincides with the largest global biotic crisis in the wake of the end-Permian mass extinction event (e.g. GALFETTI et al., 2007; SCHEYER et al., 2014a; JATTIOT et al., 2015). According to MØRK et al. (1999), the Early and Middle Triassic sediments in eastern and central Spitsbergen were deposited in a basinal setting of the Boreal Sea (Fig. 1), whereas further to the west a shallow marine environment is indicated (also see MØRK & WORSLEY, 2006).

The new specimen A/I 4363 is preserved in a large, flat, early diagenetic calcareous concretion, scattered pieces of which were collected from scree. Neither ammonoids nor conodonts have been detected in the concretion, but A/I 4363 is associated with small bivalve shells and shell fragments belonging to several different taxa (M. HAUTMANN, pers. comm.).
A/I 4363 was prepared using air pens under a binocular microscope. For some photographs, the specimen was submerged in water to enhance the contrast between the bone and the matrix. Drawings are combined from sketches produced using a camera lucida mounted on a binocular microscope, and manual tracing of structures on photographs with graphics software, under permanent consultation of the fossil. The terminology of skeletal elements follows KOGAN & ROMANO (2016).

Institutional abbreviations: PIMUZ – Palaeontological Institute and Museum, University of Zurich, Switzerland; PMU – Palaeontological collections, Museum of Evolution, Uppsala University, Sweden; SMNS – Staatliches Museum für Naturkunde Stuttgart, Germany.
Anatomical abbreviations: Af – anal fin (lepidotrichia); Ao – axonost; Bf – basal fulcrum (unpaired); Bo – baseost; ca.isv. – canal for intersegmental vessels; Cf – caudal fin (lepidotrichia); Df – dorsal fin (lepidotrichia); Dsc – dorsal scutes (mid-dorsal scales); Dlsc – dorsolateral scales; Ff – fringing fulcra; Har(l/r) – haemal arch elements (left/right); lat.ca. – lateral line sensory canal; Lsc(l/r) – mid-lateral scales (left/right); Nar(l/r) – neural arch elements (left/right); Pv – pelvic plate; Vf – pelvic fin (lepidotrichia); Vsc – ventral scutes (mid-ventral scales).

3 Systematic Palaeontology

Osteichthyes HUXLEY, 1880
Actinopterygii COPE, 1887 [sensu ROSEN et al., 1981]
Actinopteri COPE, 1872 [sensu PATTERSON, 1982]
Saurichthyidae OWEN, 1860 [sensu STENSIÖ, 1925]
Saurichthys AGASSIZ, 1834

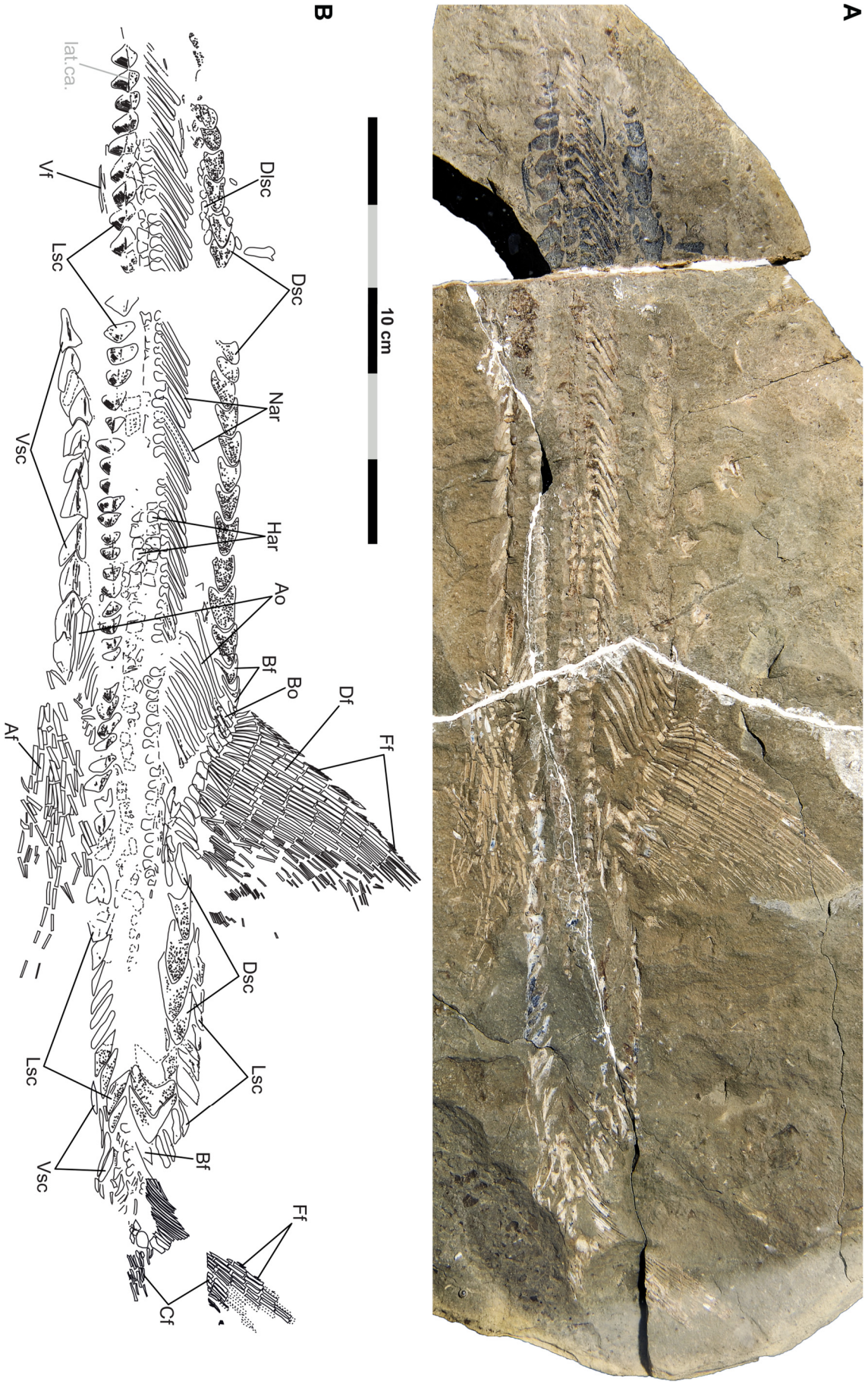
Type species: *Saurichthys apicalis* AGASSIZ, 1834 from the Ladinian (Middle Triassic) of Franconia, Germany.

Saurichthys wimani (WOODWARD, 1912)
(Figs 2–5, 6a–b)

1912 – *Belonorhynchus wimani* WOODWARD, sp. nov. – WOODWARD: 293, Pl. XIV, Figs 3–6.
1925 – *Saurichthys wimani* (A.S. WOODWARD). – STENSIÖ: 133, Pls 17–20, Pl. 26, Fig. 6.
2013 – *Saurichthys wimani* – KOGAN & ROMANO: 37, Fig. 2D.

Holotype: PMU P.293 (WOODWARD, 1912: 293–295, Pl. XIV, Figs 3–4), partial skull and anteriormost body portion with pectoral fins and parts of the squamation (Fig. 5).

Material: PIMUZ A/I 4363 comprises the posterior half of a saurichthyid trunk and displays elements of the axial skeleton, several scale rows, parts of the pelvic girdle, the dorsal, anal and the caudal fin. The skeletal elements are mostly preserved in situ. The nodule was scattered into several pieces in the field, which could be glued together to four parts (a, b, c, d). Other parts of the fossil could not be retrieved in the field. A/I 4363 is preserved as part (A/I 4363a, Figs 2, 6a–b) and partial counterparts (A/I 4363b, A/I 4363c, A/I 4363d, Figs 3–4), in which part d lies between the anterior portions of parts a and b, preserving the counterparts to the skeletal elements of both a


A
B
10 cm
lat.ca.
Vf
Dlsc
Lsc
Dsc
Nar
Vsc
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Ao
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Cf

and b. The specimen is flattened laterally, but the left side is slightly displaced dorsally against the right side, which is most obvious in the dorsoventrally flattened caudal peduncle, but also in the position of the pelvic fins and the left and right arcual ossifications. The fragmentary preservation of the ventral fins on part b contrasts with the delicate appearance of elements on part a, suggesting that the carcass was buried lying on its right side, with its left side covered by sediment and more easily disturbed by currents.

Locality and stratigraphy: From the Smithian (early Olenekian, Early Triassic) 'fish horizon' (Lusitaniadalen Member, Vikinghøgda Formation) of Stensiöfjellet, Sassendalen, east-central Spitsbergen, Svalbard, Norway (Fig. 1).

Description: PIMUZ A/I 4363 encompasses the posterior body part from a short distance anterior to the pelvic girdle up to the caudal fin. The length of this body portion measures about 320 mm, suggesting a total length of at least 80 cm for the whole animal (cf. KOGAN & ROMANO, 2016).

Squamation: As typical for many saurichthyids, A/I 4363 exhibits longitudinal rows of scales in mid-dorsal, mid-ventral and mid-lateral position (Figs 2–4). Several additional scales are seen ventrally to the mid-dorsal ones; a ventrolateral scale row, on the contrary, is not observed in the preserved body portion.
On part a and b of the concretion (Figs 2–3), twenty mid-dorsal scales (scutes) are preserved anterior to the dorsal fin, with about three further scales lost near the middle of this row. The free field of these scales, seen as impression on part a, is heart-shaped, ornamented with tubercles and longer than broad. The inside of each scale, visible on part b, bears a distinct longitudinal keel for articulation with the following preceding scute. Over the body, the length of the mid-dorsal scales increases posteriad, with the longest scute preserved in front of the dorsal fin (its free field being ca. 14 mm long and 6 mm wide). The dorsal fin is preceded by two to three distinctly smaller, V-shaped scales, which can be interpreted as unpaired basal fulcra sensu ARRATIA (2009). Posterior to the dorsal fin, the mid-dorsal scale row resumes with two symmetrical elements enclosing the hindmost rays of this fin (Figs 2, 6a–b). At least seven scutes are developed between these paired elements and the beginning of the caudal fin, the posterior three of which being distinctly broader than long. Because of the width of these precaudal scutes, the caudal peduncle is slightly twisted and flattened in dorsoventral rather than in lateral direction. Posterior to the precaudal scutes lies another, much more delicate element, probably representing an unpaired basal fulcrum.
The mid-ventral scale row is less well preserved, with only 13 scutes discernible anterior to the anal fin on parts a (Fig. 2) and d. The scales are seen as impressions of their inside on part a. On part d, two mid-ventral scales are preserved in external view. They appear more slender than those on part a and, thus, could pertain to the anal loop. Five or six mid-ventral scutes are also visible anterior to the caudal fin (Figs 2, 6a–b). The mid-ventral scutes have the same general appearance as the corresponding mid-dorsal ones, but their fragmentary preservation precludes a more detailed description.
The mid-lateral scales are more numerous than the mid-dorsal and mid-ventral ones, but the exact numerical relationship cannot be established. There are about 39 mid-lateral scales up to the hind margin of the dorsal fin, where the torsion of the caudal peduncle occurs. Posterior to this level, about 16 mid-lateral scales are preserved on the right side of the caudal peduncle, whereas those from the left flank (approximately 13) are now situated dorsal to the mid-dorsal precaudal scutes. The mid-lateral scale row continues until the end of the tail (Fig. 6a–b). The mid-lateral scales relate as 1:2 to the dorsal elements of the axial skeleton (neural arches; Figs 2–4). The scales are quite large (ca. 4 mm long and 5 mm high at the level of the pelvic fins), anteriorly inclined, and rhombic to bow-shaped in outline. The course of the lateral line sensory canal divides the free field of the scales near the middle into a tuberculated dorsal and a subvertically striated ventral portion. The mid-lateral scales of the caudal peduncle deviate from that morphology in being dorsoventrally elongate and bearing only a tuberculate ornamentation, while the ventral part seems to be reduced to a series of denticles pointing posteriorly (Fig. 6a–b). On the caudal fin, the mid-lateral scales appear bow-shaped and small.
Additional scales are preserved ventral to the mid-dorsal scale row, predominantly in the anterior part of the fossil (Figs 2, 4a–b). Some isolated dorsolateral scales also occur between the pelvic fins and the dorsal fin (Figs 3, 4c–d). The dorsolateral scales are small, ovoid to rhombic in outline, ornamented with fine tubercles, and arranged in oblique rows, running from anterodorsal to posteroventral.

Fig. 2: *Saurichthys wimani* (WOODWARD, 1912) from Mount Stensiö, Vikinghøgda Formation (Early Triassic) of Spitsbergen. A – part a of PIMUZ A/I 4363; B – interpretive drawing of the skeletal elements thereof. Anterior to the left.

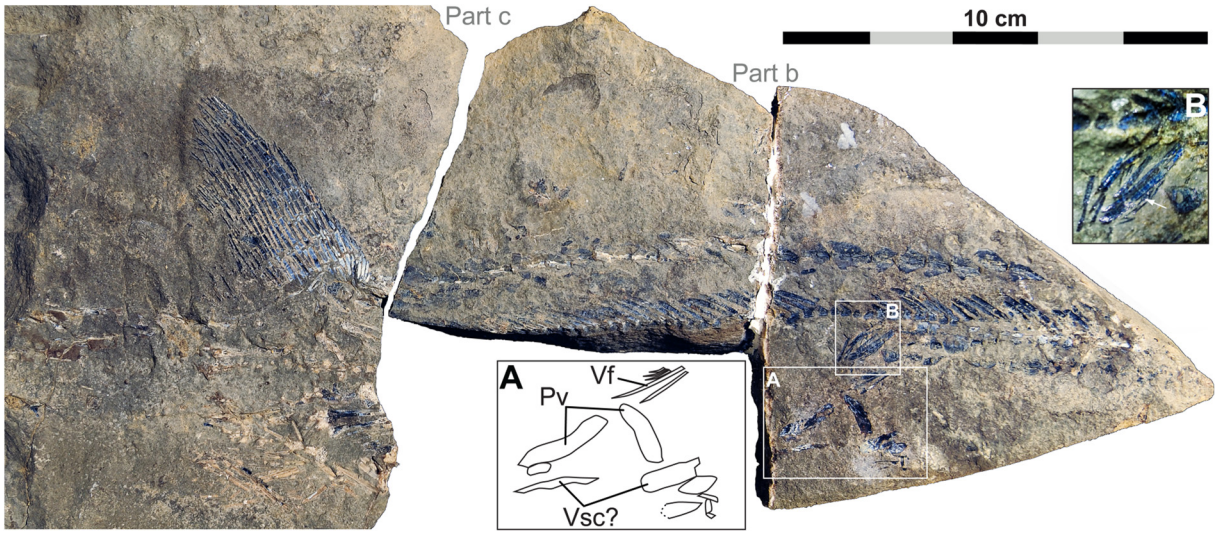


Fig. 3: *Saurichthys wimani* (WOODWARD, 1912). Part b and c of PIMUZ A/I 4363. Parts b and c are not in natural configuration, and the counterpart of the caudal fin is missing on part c; A– interpretive drawing of the disarticulated endochondral pelvic girdle; B – close-up view of one of the pelvic fins, with fringing fulcra indicated by the white arrow. Anterior to the right.

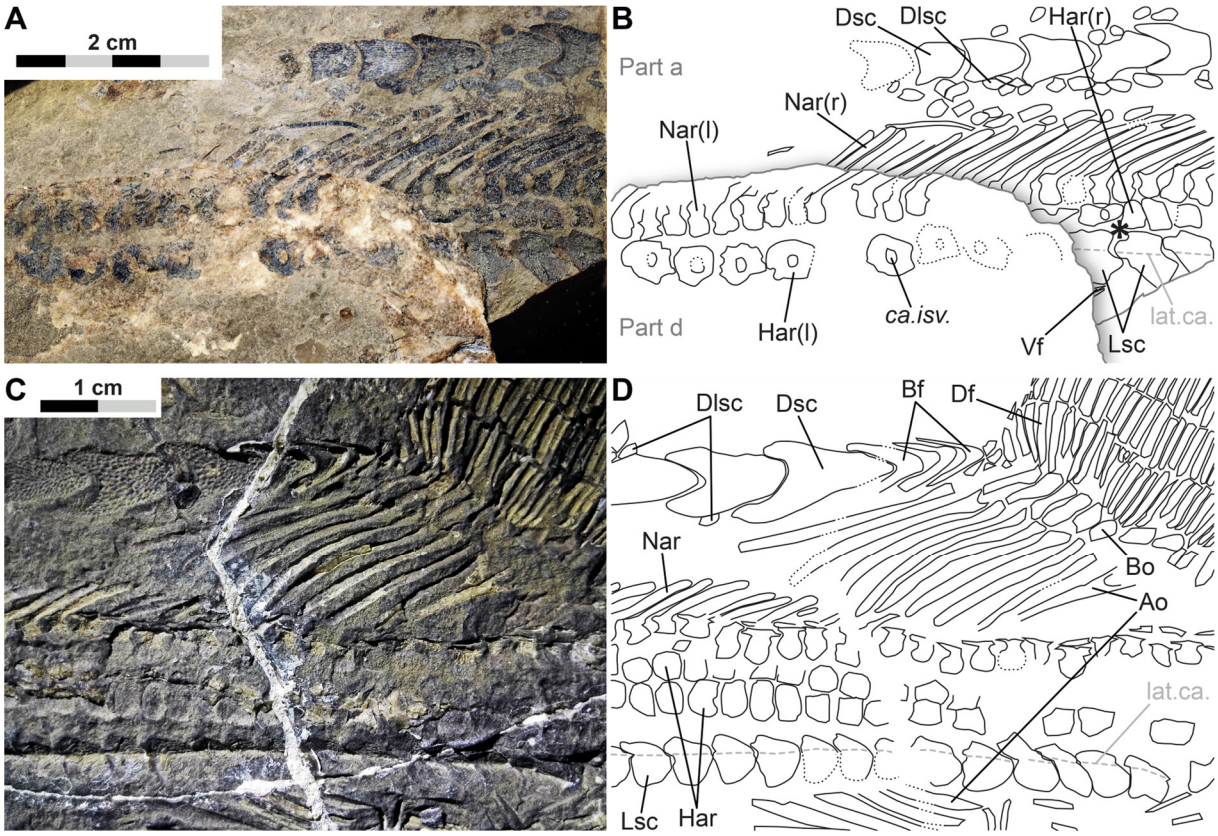


Fig. 4: *Saurichthys wimani* (WOODWARD, 1912). A – parts a and d of PIMUZ A/I 4363 in natural arrangement to each other, showing the skeleton in the region of the abdominal-caudal transition (fossil submerged in water); B – interpretive drawing of the skeletal elements in A; C – part a of A/I 4363 at the level of the dorsal/anal fin, showing the change in morphology of the neural arches; D – interpretive drawing of the skeletal elements in C. The asterisk in B marks the change in the ratio between the neural and haemal arches, from a 2:1 to a 2:2 relationship, at the abdominal-caudal transition (sensu MAXWELL & WILSON, 2013). See text for details. Anterior to the left.

Fins: The pelvic and all unpaired fins are preserved. The pelvic fins are visible on parts a, b and d (Figs 2–4). Apart from some lepidotrichia, the elements of the ventral fins are disarticulated. A few small fringing fulcra are observed along the leading margin of one of these fins (Fig. 3b). Probably, both dislocated pelvic plates are preserved on part b (Fig. 3a). These bones are elongate and plate-like. Other, nearby bones could correspond to ossified metapterygial elements or radials (cf. STENSIÖ, 1925), but they are too incompletely preserved for description. The fin rays contain a long, unsegmented basal portion, but are probably distally segmented.
The dorsal fin (Figs 2–4) is supported by at least nine elongate proximal radials (axonosts) and a series of at least 14 subrectangular distal radials (baseosts). The exoskeletal part consists of no less than 34 lepidotrichia, the longest of which comprise eight to nine segments of similar length. At least the longer fin rays bifurcate distally, about two or three times. A series of about 30 fringing fulcra of ARRATIA's (2009) Pattern C is seen along the leading edge of the fin.
The anal fin (Figs 2–3) has been deformed during burial. Although less well-preserved, it seems to correspond morphologically to the opposed dorsal fin. At least five axonosts are exposed, and the first one appears to be more massive than the following ones. Baseosts are possibly visible on part c of the fossil. The longest lepidotrichia consist of no less than ten to eleven somewhat equally long segments, hence the same segmentation pattern as for the dorsal fin.
The caudal fin is fragmentarily preserved (Figs 2, 6a–b). Two patches composed of at least 16 lepidotrichia belong to the dorsal caudal lobe. Each fin ray of the dorsal lobe is subdivided into several elongate units of comparable length, except for the basalmost segment, which is always longer. The segmentation pattern is reminiscent of that of the dorsal fin. Branching is observed distally on the posterior lepidotrichia. A third, smaller patch of about seven incomplete, somewhat disarticulated fin rays, lying posterior to the last scales of the mid-lateral row, probably belongs to the central part of the caudal fin web, whereas the ventral caudal lobe appears to be missing.

Axial skeleton: The persistent notochord was surrounded by left-right pairs of dorsal and ventral arcualia, preserved on all four parts of A/I 4363. On part a (Figs 2, 4), the incomplete series of dorsal elements comprises about 70 neural arches, each consisting of a rounded base (pedicle) and two to three projections pointing in cranial, dorsocaudal and caudal direction. The rather small process directed anteriorly is referred to as the praezygapophysis (see e.g. RIEPPEL, 1985; TINTORI, 1990). The much longer, dorsocaudally ascending projection is traditionally termed neural spine (e.g. STENSIÖ, 1925; TINTORI, 1990), although it may not be homologous with the unpaired neural spines of higher vertebrates. The short, nearly horizontal posterior projection is termed postzygapophysis (RIEPPEL, 1985; TINTORI, 1990). While praezygapophyses and neural spines are developed from the anterior end of the fossil until the dorsal fin, postzygapophyses appear to be absent in the abdominal and anterior caudal part of the vertebral column. The first distinctive postzygapophyses are developed on the neural arches situated at the level of the first dorsal axonost, where they are similar in size to the praezygapophyses. The neural spines become gradually shorter in caudal direction, and more rapidly so within the anterior portion of the dorsal fin support. At the level of the fifth to sixth dorsal axonost, the morphology of the neural arcualia changes abruptly and no neural spines are observed posterior to this point. The posterior caudal neural arches are small and T-shaped, with two horizontal projections of nearly equal length that are interpreted as prae- and postzygapophyses (Figs 4c–d, 6a–b).
The ventral arcual elements, too, exhibit a change in morphology along the body. On part d (Fig. 4a–b), which comprises the most anterior portion of the vertebral column as preserved in A/I 4363, these ventral elements are subrectangular in lateral outline and they correspond as 1:2 to the neural arches. Near their centre, they are pierced by a foramen for intersegmental vessels (cf. STENSIÖ, 1925). Further caudally, the ventral arcual ossifications are smaller and relate to the dorsal vertebral elements as 1:1. This change in ratio between the neural and haemal arches is located just caudal to the pelvic fins, near the position of the pelvic plates on part b, and corresponds to the osteological abdominal-caudal transition sensu MAXWELL & WILSON (2013). None of the haemal arches exhibits haemal spines. The preservation of the haemal arches in the caudal peduncle is too fragmentary for a sound description.

4 Discussion

For almost a decade, saurichthyids have attracted increased interest by researchers studying various palaeobiological and evolutionary aspects of fossil actinopterygians (MUTTER et al., 2008; KOGAN et al., 2009, 2015; RENESTO & STOCKAR, 2009, 2015; WU et al., 2009, 2011, 2013, 2015; SCHMID & SÁNCHEZ-VILLAGRA, 2010; KOGAN, 2011; ROMANO et al., 2012; MAXWELL & WILSON, 2013; MAXWELL et al., 2013, 2015, 2016; TINTORI, 2013; WILSON et al., 2013; SCHEYER et al., 2014b; TINTORI et al., 2014b; WERNEBURG et al., 2014; ARGYRIOU et al., 2016; BEARDMORE & FURRER, 2016; KOGAN & ROMANO, 2016). Saurichthyids constitute ideal study organisms among early Mesozoic vertebrates to address macroevolutionary questions due to their (1) extended fossil record (latest Permian–Middle Jurassic, ~75 million years), (2) global distribution, (3) high species

richness (with often several species occurring at the same locality), (4) representation by abundant material in many fish assemblages, (5) unique anatomy (allowing identification of even fragmentary specimens at least at the genus level), and (6) reproductive and locomotor specializations. While the species from Middle Triassic Tethyan Lagerstätten (Monte San Giorgio, Grigna Mountains, Luoping Biota) are better-studied (e.g. RIEPPEL, 1985; RENESTO & STOCKAR, 2009, 2015; WU et al., 2009, 2011, 2015; MAXWELL et al., 2013, 2015; TINTORI, 2013), still little is known about early saurichthyids (Changhsingian–Spathian; e.g. ROMANO et al., 2012; KOGAN & ROMANO, 2016) and late saurichthyids (Carnian–Aalenian; e.g. TINTORI & GOZZI, 2005; MAXWELL, 2016; KOGAN et al., in prep.).

Spitsbergen is one of the longest-known localities yielding early saurichthyids. Early Triassic fishes from Spitsbergen have been discovered in the mid-19th century (e.g. BRINKMANN et al., 2010; KEAR et al., 2016) and were extensively studied about a century ago (WOODWARD, 1912; STENSIÖ, 1918, 1919, 1921, 1925, 1932). With the exception of SCHWARZ (1970), no new taxonomic studies on the osteichthyans from the Early Triassic of Spitsbergen have been published since 1925, whereas chondrichthyans received some interest (e.g. BIRKENMAJER & JERZMAŃSKA, 1979; BŁAŻEJOWSKI, 2004; ROMANO & BRINKMANN, 2010). New osteichthyan material was, however, mentioned or figured in some recent publications (e.g. COX & SMITH, 1973; SCHEYER et al., 2014a), and some taxa have been restudied anatomically (e.g. STENSIÖ, 1932; VÉRAN, 1988, 1995, 1996).

Four *Saurichthys* species are known from the Early Triassic of Spitsbergen: *S. wimani* (WOODWARD, 1912), *S. ornatus* STENSIÖ, 1925, *S. elongatus* STENSIÖ, 1925 and *S. hamiltoni* STENSIÖ, 1925. Further saurichthyid remains have been described by STENSIÖ (1925) either without species-level identification or with unsure species attribution. Articulated material of *Saurichthys* from Spitsbergen is mainly restricted to the Smithian 'fish horizon', although according to STENSIÖ (1925) a few fossils have been found in strata "somewhat above this horizon" (STENSIÖ, 1925: p. 153), which would thus be of late Smithian or Spathian age (WEITSCHAT & DAGYS, 1989; MØRK et al., 1999; MØRK & WORSLEY, 2006; Table 1) rather than Middle Triassic (contra KEAR et al., 2016).

A revision of STENSIÖ's (1925) species and diagnoses in light of new finds from the Vikinghøgda Formation and additional comparative data requires restudy of the original specimens, which is beyond the scope of present paper. Therefore, attribution of PIMUZ A/I 4363 to a species has to rely on literature data and accessible illustrations and must for now be regarded as provisional.

The most comprehensively described Spitsbergen species is *S. ornatus*. This taxon is based on numerous essentially cranial remains and one isolated mid-body segment (PMU P.338), the latter referred to *S. ornatus* with hesitation by STENSIÖ (1925). Individual P.338 (STENSIÖ, 1925: Pl. 15–16, Figs 1–5) shows the posterior abdominal and anterior caudal region, characterized by small mid-dorsal, mid-ventral and mid-lateral scales, fairly large fringing fulcra on the pelvic fins and a 1:2 relationship of ventral and dorsal arcualia throughout the vertebral column – conditions that clearly deviate from those in A/I 4363. Furthermore, STENSIÖ (1925) reported a numerical relationship of mid-dorsal, mid-lateral and mid-ventral scales and neural arches of 1:2:2:2, meaning that the mid-lateral scales are as numerous as the dorsal vertebral elements and the mid-ventral scales twice as numerous as the mid-dorsal ones. If true, this relationship would be unique among saurichthyids. Whereas it is often difficult to establish the ratio between the axial skeleton and the mid-dorsal or mid-ventral scales, which vary both in size and in number, the relationship of mid-lateral scales to neural arches remains constant throughout the body in saurichthyids (IK pers. obs.).

The largest Spitsbergen postcranium segment hitherto known, PMU P.330, was described in detail by STENSIÖ (1925), albeit with some taxonomic uncertainty. While in the text it is classified as "indeterminable as to species" (STENSIÖ, 1925: 172ff), P.330 is labelled as *S. ornatus* in the caption of the plate (STENSIÖ, 1925: Pl. 15–16, Fig. 6). This ca. 22 cm long fossil shows the posterior abdominal portion and the anterior caudal segment until the hind margin of the dorsal fin. The ratio between the neural and haemal arches remains as 2:1 throughout the preserved body part, the mid-dorsal scales appear narrow, and the mid-lateral scales are very small – characters reminiscent of P.338, but clearly different from PIMUZ A/I 4363. A peculiar feature of P.330, documented by STENSIÖ (1925: 172), is the presence of two haemal spines per haemal arch. This character – which according to F.-X. WU (pers. comm.) may be a misinterpretation of anal axonosts – is absent in P.388 and has elsewhere only been observed in the Middle Triassic *Saurichthys yangjuanensis* WU et al., 2015, from southern China (see below). Another postcranial remain, PMU P.337, is a fragment of the axial skeleton, referred to *Saurichthys* sp. by STENSIÖ (1925) but without a detailed description or figure.

Both *S. wimani* and *S. elongatus* are known from skulls and anterior body portions, including the pectoral girdle and fins, elements of the axial skeleton, and the anteriormost squamation, whereas the postcranium of *S. hamiltoni* is entirely unknown (WOODWARD, 1912; STENSIÖ, 1925). STENSIÖ (1925) lists three specimens of *S. elongatus* with postcranial elements present (PMU P.271, P.278 and P.699), but of them only P.271 (lectotype; ROMANO et al., 2012) has been depicted in the original publication (STENSIÖ, 1925: Pl. 22, Fig. 4, Pl. 23, Figs 1–2; Pl. 25, Figs 3–4; Pl. 34, Fig. 1). Characteristic features of *S. elongatus* include large mid-lateral scales, broad mid-dorsal scales, but narrow mid-ventral scales – the last mentioned trait being different from the broad mid-ventral scales of A/I 4363.

The only specimen of *S. wimani* hitherto known showing postcranial characters is the holotype PMU P.293 (Fig. 5). Descriptions by WOODWARD (1912) and STENSIÖ (1925) reveal that the mid-dorsal and mid-ventral scales of P.293 are broad, the mid-lateral scales are high in the anterior part of the body and should decrease in height farther posteriorly (cf. KOGAN & ROMANO, 2016), and additional rows of scales are present in dorsolateral position. As noted by STENSIÖ (1925), the mid-lateral scales seemingly correspond in number to the mid-dorsal ones, at least in the anterior body part of *S. wimani*, indicating a 1:2 relationship between the mid-lateral scales and neural arches. Alongside *S. elongatus*, *S. wimani* was the only saurichthyid for which segmented pectoral fins have been described (WOODWARD, 1912; STENSIÖ, 1925; Fig. 5), an observation that has long been overlooked by authors (RIEPPEL, 1985; SCHMID & SÁNCHEZ-VILLAGRA, 2010; ROMANO et al., 2012), until evidence of segmented pectoral fin rays was presented for *S. madagascariensis* PIVETEAU, 1945 (KOGAN & ROMANO, 2016). Finally, size estimates for *S. wimani* indicate a head length of about 25 cm and a total body length of 75–100 cm (STENSIÖ, 1925; ROMANO et al., 2016) – a range in which A/I 4363 would fall.

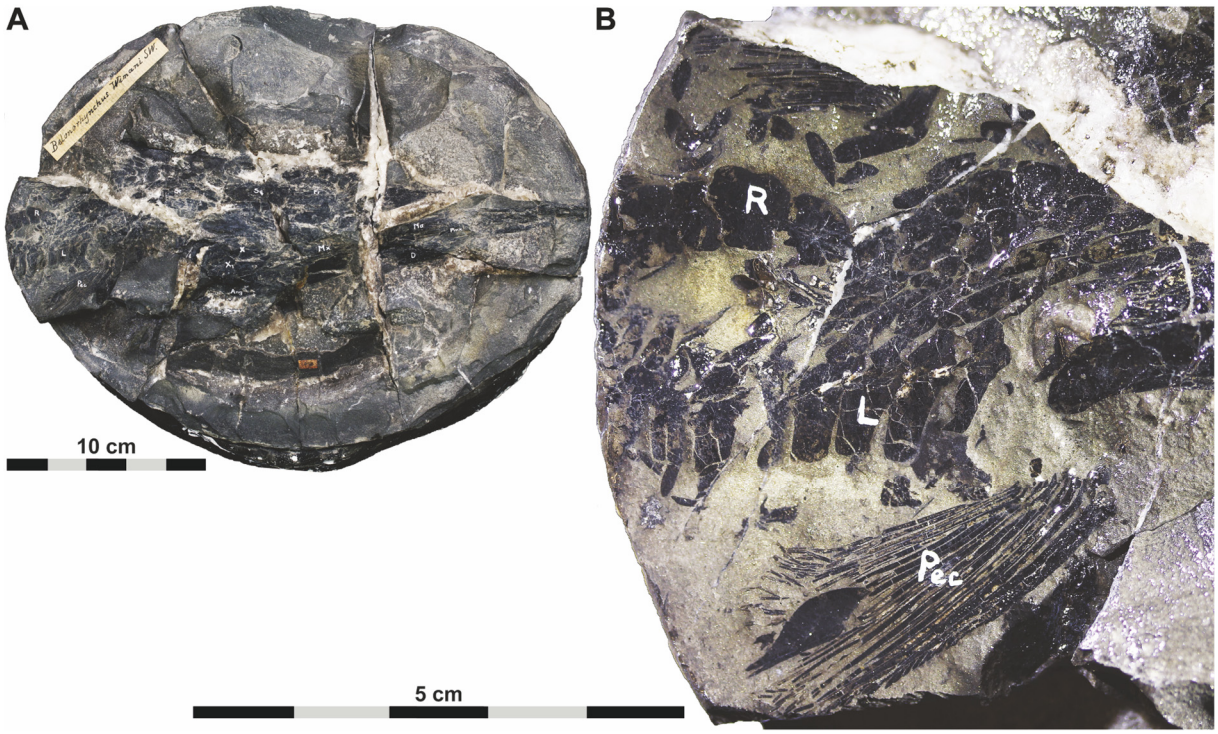


Fig. 5: *Saurichthys wimani* (WOODWARD, 1912). A – holotype PMU P.293 (counterparts of nodule not shown) from the Early Triassic of Sassen Bay, Spitsbergen; B – magnified view of the anterior postcranium of P.293 (contrast enhanced with water). Anterior to the right. Abbreviations marked on the fossil in B: L, mid-lateral scale; Pec, pectoral fin; R, mid-dorsal scale. Picture courtesy F.-X. WU.

Based on the current state of knowledge, we consider the evidence sufficient to refer A/I 4363 to *S. wimani*. Due to distinct morphological differences, an allocation to *S. ornatus* or *S. elongatus* is excluded and the use of open nomenclature appears unnecessary. We emphasize, nonetheless, the necessity of a sound taxonomic revision for the Spitsbergen saurichthyids along with other osteichthyan taxa. Specimen A/I 4363 represents the first occurrence of *S. wimani* on Mt. Stensiö, which already has yielded *S. ornatus*, *S. elongatus* and *S. hamiltoni* (Fig. 1c). Our description and review confirm that at least three species of *Saurichthys* can be reliably distinguished in the 'fish horizon' of Spitsbergen by their postcranial morphology.

S. wimani broadly conforms to the early saurichthyid morphotype as proposed by KOGAN & ROMANO (2016). Regarding the structure of the fins, consisting of segmented and branched lepidotrichia and being equipped with fringing fulcra along the leading fin margins, *S. wimani* is comparable with *S. madagascariensis* (Early Triassic, Madagascar; KOGAN & ROMANO, 2016) and, as far as preserved, *S.* aff. *dayi* (Early Triassic, Greenland; KOGAN, 2011). The endoskeletal supports of the fins of A/I 4363, too, show no apparent difference to other early saurichthyids. In the marine realm, the early saurichthyid morphotype is restricted to species of Changhsingian–Smithian age (latest Permian to mid-Early Triassic; ROMANO et al., 2012; KOGAN & ROMANO, 2016), suggesting an early radiation followed by selective extinction, possibly in conjunction with the late Smithian biotic crisis (e.g.

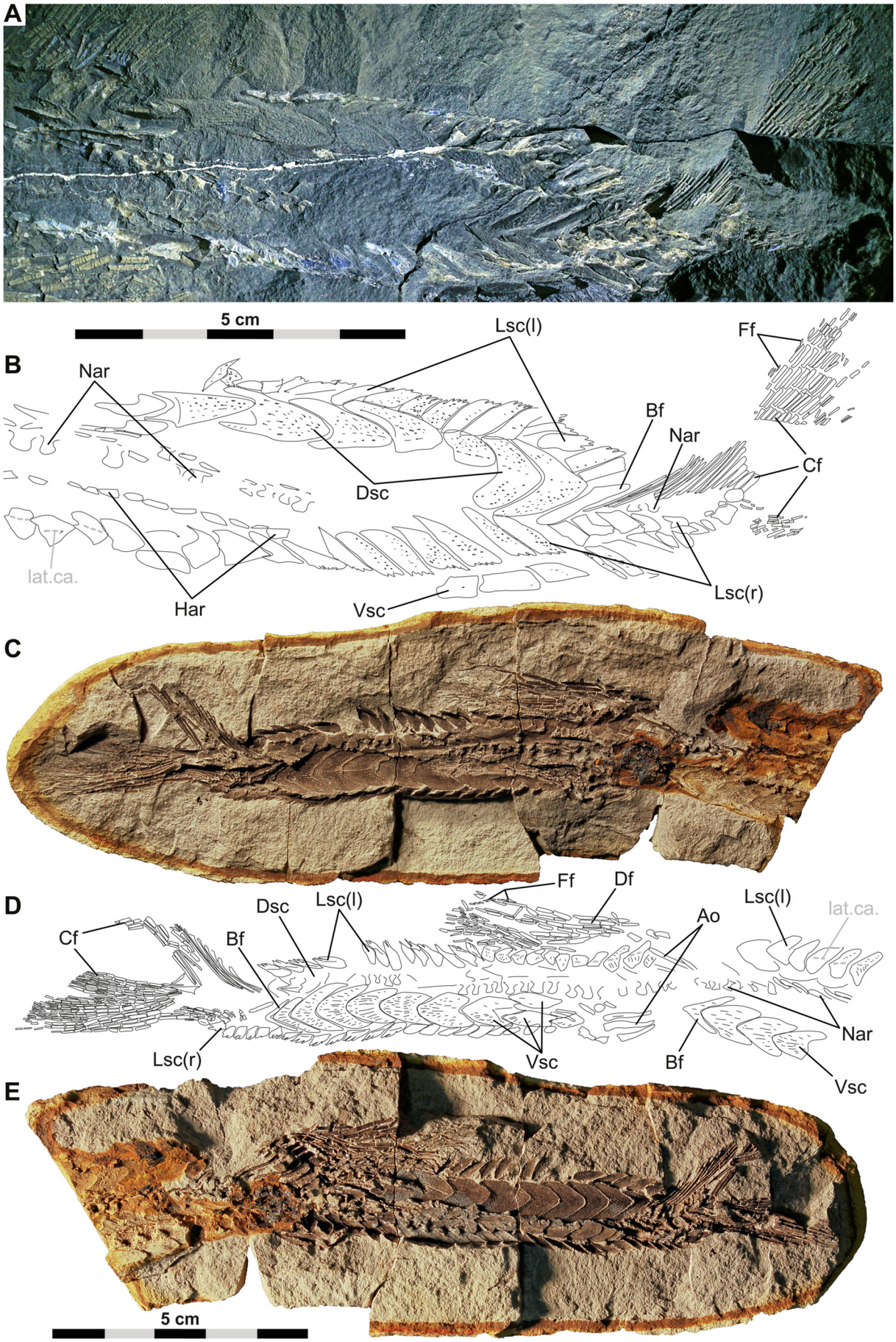
GALFETTI et al., 2007). Post-Smithian species approaching the early saurichthyid morphotype occur, however, in freshwater settings, which may have served as refugia (e.g. KOGAN et al., 2009; ROMANO et al., 2012).

From an evolutionary perspective, A/I 4363 bears interesting information on the axial skeleton and the squamation. It is one of the few early saurichthyids – and the first one from Spitsbergen – to clearly show the switch from a 2:1 neural arch to haemal arch pattern to a 2:2 pattern. Early Triassic evidence for this morphology change has been reviewed by KOGAN & ROMANO (2016), who detected this change at the level of the osteological abdominal-caudal transition (ACT) in *S. madagascariensis* and hypothesized the presence of the same pattern in other early saurichthyids. In Middle Triassic species, such a change has been documented in *S. rieppeli* MAXWELL et al., 2015 (Monte San Giorgio, Switzerland), at the mid-level of the anal fin base, thus posterior to the ACT. Furthermore, WU et al. (2015) described three different haemal arch morphologies (their morphotypes 1–3) in the caudal region of *S. yangjuanensis*. They termed the 2:1 neural to haemal arch pattern morphotype 3, where no or just one haemal spine is present per haemal arch; a 2:1 pattern with two haemal spines per haemal arch was called morphotype 2; and the 2:2 neural to haemal arch pattern morphotype 1. Morphotype 2 is interpreted as an intermediary stage between type 3 and type 1, and WU et al. (2015) suggest that the change from one of these character states to another occurs at a rather late ontogenetic stage. Since no abdominal haemal arches are preserved in *S. yangjuanensis*, this observation is hard to correlate with the position of the ACT, and it appears unclear in which direction (craniad or caudad) this change occurred. It is noteworthy, nevertheless, that the fragment PMU P.338, exhibiting haemal arches of morphotype 3, represents an individual of larger body size than P.330, which shows haemal arches of morphotype 2 (according to STENSIÖ, 1925), thus suggesting a later ontogenetic stage and implying that the two fossils may not be conspecific.

The squamation of A/I 4363 exhibits two particularities. At first glance, there is little deviation from the early saurichthyid morphotype, characterized by large, broad, interlocking mid-dorsal and mid-ventral scutes, high mid-lateral scales showing the typical bipartite ornamentation, and further scales in dorsolateral position. However, we find no evidence of ventrolateral scales in A/I 4363, which in *S.* aff. *dayi*, *S. madagascariensis* and *S.* aff. *madagascariensis* would extend at least until the pelvic fins (KOGAN, 2011; KOGAN & ROMANO, 2016). Additionally, the mid-lateral scales of the caudal peduncle of A/I 4363 show an unusual change in morphology, exhibiting a row of denticles at their caudoventral margin (Fig. 6a–b). Denticles are frequently found at the caudal margin of actinopterygian scales (SCHULTZE, 1966), but have never been described in this position in saurichthyids, which were previously known to only feature small spines along the scale midline (RIEPPEL, 1985; WU et al., 2015; KOGAN & ROMANO, 2016). A similar pattern as in PIMUZ A/I 4363 occurs in SMNS 80405 (Fig. 6c–e) from Northwest Madagascar, a posterior postcranial segment preserved in dorsoventral view as part and counterpart, which we refer here to *Saurichthys* cf. *madagascariensis*. The caudal peduncle of SMNS 80405 exhibits nine mid-dorsal and mid-ventral scutes, including the first, paired element embracing the bases of the dorsal and the anal fin, respectively. The posteriormost of these precaudal scutes is shorter than the preceding ones and could be regarded as the first caudal basal fulcrum (attributable to Pattern II of ARRATIA, 2009). About 26 right and about 23 left mid-lateral scales can be observed between the dorsal and anal fins and the tail fin. The anterior of these show the 'normal' morphology composed of a tuberculated dorsal and a striated ventral part, separated by the course of the lateral line sensory canal, but at a level about ten scales behind the first dorsal and anal axonosts, the striated ventral part is suddenly lost and instead three to four ventrocaudally directed denticles appear.

At present, the data are insufficient to allow conclusions about the functional, developmental or taxonomic significance of these denticles, or to suggest any kind of dimorphism. It is worth noting that STENSIÖ (1932) demonstrated the loss of denticles on the caudal margin of the scales of "*Perleidus*" *stoschiensis* and *Broughia perleididoides* (Early Triassic, Greenland) during ontogeny. Nonetheless, a homology with the denticles on the scales of the caudal peduncle of *Saurichthys* requires further comparative studies.

Fig. 6: Tails of two Early Triassic saurichthyids. A–B – *Saurichthys wimani* (WOODWARD, 1912): caudal portion of PIMUZ A/I 4363a (A) and interpretive drawing thereof (B). C–E – *Saurichthys* cf. *madagascariensis* PIVETEAU, 1945 from the Ambilobe Basin, Northwest Madagascar: SMNS 80405, part a (C), interpretive drawing of part a (D), and counterpart SMNS 80405b (E). Anterior to the left in A, B and E, and to the right in C and D.


A
5 cm
B
Nar
Lsc(l)
Ff
Bf
Nar
Cf
Dsc
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D
Ff
Df
Dsc
Lsc(l)
Lsc(l)
lat.ca.
Cf
Bf
Ao
Nar
Lsc(r)
Vsc
Bf
Vsc
E
5 cm

5 Concluding remarks

The new specimen PIMUZ A/I 4363 is ascribed to *Saurichthys wimani* (WOODWARD, 1912) based on similarities in the squamation pattern with the holotype. The postcranium of *S. wimani* is now characterized by (1) segmented, branched lepidotrichia and small fringing fulcra on all fins, (2) four longitudinal rows of large, ornamented scales in mid-dorsal, mid-ventral and mid-lateral position and small, ornamented rhombic dorsolateral scales (the ventrolateral scale row is probably absent), and (3) a vertebral column composed of neural arches that relate as 2:1 to the mid-lateral scales, as 2:1 to the haemal arches in the abdominal segment and as 2:2 in the caudal body portion. Consecutive mid-dorsal and mid-ventral scales articulate with each other via a system of interlocking keels and grooves, and the mid-lateral scales are divided by the lateral line sensory canal into a tuberculated dorsal portion and a vertically striated ventral part. Therefore, the anatomy of *S. wimani* generally conforms to the early saurichthyid morphotype (sensu KOGAN & ROMANO, 2016). The caudal peduncle of A/I 4363, along with that of a specimen referred to *Saurichthys* cf. *madagascariensis*, shows peculiar mid-lateral scales with caudally pointing denticles on their ventrocaudal margin (Fig. 6), a pattern that yet has not been described in saurichthyids.
Specimen A/I 4363 is only the eighth saurichthyid postcranium from the Early Triassic of Spitsbergen and the most complete one known so far. The four *Saurichthys* species hitherto described from that locality have been differentiated mainly on the basis of cranial features; however, our survey of postcranial character distribution supports the distinction of at least three species in the Smithian 'fish horizon'. Irrespective of the necessity for a taxonomic revision of the Spitsbergen saurichthyids, this conclusion provides further evidence for the view that saurichthyids were already diverse in the Early Triassic (MUTTER et al. 2008; ROMANO et al., 2012), even at the locality level.

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